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Author(s): Niels P. R. Anten, Miguel Martínez-Ramos and David D. Ackerly

Reviewed work(s):

Source: *Ecology*, Vol. 84, No. 11 (Nov., 2003), pp. 2905-2918

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/3449961>

Accessed: 03/10/2012 13:42

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DEFOLIATION AND GROWTH IN AN UNDERSTORY PALM: QUANTIFYING THE CONTRIBUTIONS OF COMPENSATORY RESPONSES

NIELS P. R. ANTEN,^{1,3} MIGUEL MARTÍNEZ-RAMOS,² AND DAVID D. ACKERLY¹

¹Department of Biological Sciences, Stanford University, Stanford, California 94305-5020 USA

²Centro de Ecología, Universidad Nacional Autónoma de México, Ap. Post. 27–5, CP 58089, Morelia, Mexico

Abstract. We analyzed to what extent and by what mechanisms plants of the tropical understory palm *Chamaedorea elegans* are able to mitigate the negative effects of defoliation on performance (i.e., plant size, total growth, leaf lamina growth, and reproduction) and how this is related to light availability. For this purpose we developed a new approach that allowed us to quantify the performance of defoliated plants relative not only to the performance of undamaged plants, but also relative to the estimated performance of hypothetical defoliated plants that do not exhibit any mechanisms of compensatory growth. The latter provides a way to quantify the adaptive value of compensation with reference to a hypothetical noncompensating alternative state. *C. elegans* plants were grown in a greenhouse at two light levels (5% and 16% of natural daylight) and subjected to five defoliation treatments (a control and four levels of defoliation). Defoliation was repeated every three months. Growth analysis revealed that defoliated plants allocated considerably more mass to the production of leaf laminae (f_{lam}) than control plants, at the expense of allocation to other organs, particularly reproductive structures. Average growth rates per unit leaf area (NAR) and per unit plant mass (RGR), both measured on the basis of above-ground mass, increased with the level of defoliation at high light but not at low light. We estimated that the increases in f_{lam} and NAR enabled *C. elegans* to compensate for part of the potential loss in performance caused by defoliation, even in cases where their RGR values were lower than those of control plants. Sensitivity analysis indicated that changes in NAR contributed more to this compensation than f_{lam} , but the importance of f_{lam} increased with defoliation level and with decreasing light availability. The degree of compensation was higher in the high- than in the low-light treatment, suggesting that the possession of traits associated with compensatory growth may be more important in sunny than in shaded environments. The degree of compensation differed depending on the measure of performance. Defoliated plants fully compensated for the potential reduction in lamina growth but compensated for <20% of estimated loss in reproductive output. Since survival of *C. elegans* plants appears to be strongly associated with their total leaf area, the greater compensation for lamina growth is important in relation to population dynamics.

Key words: biomass allocation; *Chamaedorea elegans*; compensatory growth; defoliation; growth analysis; herbivory; non-timber forest products; reproductive allocation; specific leaf area; tropical rain forest.

INTRODUCTION

Plants are often subjected to partial defoliation caused by herbivores (wild and domestic) or by physical damage from falling canopy debris or storms (McNaughton 1983, Marquis 1984, Chazdon 1991). Humans also harvest leaves from a number of plant species for various purposes (see Nations 1992). Partial defoliation entails a loss of photosynthetically active

tissue and can therefore negatively affect growth, reproduction and survival of plants (Karban and Strauss 1993).

The consequences of defoliation for growth, reproduction and survival depend on the severity with which it occurs and the ability of plants to mitigate its effects through compensatory growth (Trumble et al. 1993). Plant growth analysis can be used to assess the contributions of different mechanisms of compensatory growth to relative growth rate (RGR, growth per unit whole plant biomass) via its two components: net assimilation rate (NAR, growth per unit leaf area) and leaf area ratio (LAR, leaf area per total biomass) ($\text{RGR} = \text{NAR} \times \text{LAR}$). Defoliation may have direct positive impacts on growth, partially mitigating the loss of leaf area, e.g., by increased light penetration in the canopy (Gold

Manuscript received 26 July 2002; revised 5 February 2003; accepted 9 February 2003; final version received 6 March 2003. Corresponding Editor: M. J. Lechowicz.

³ Present address: Department of Plant Ecology, Utrecht University, P.O. Box 800.84 NL-3508 TB Utrecht and Chair Group of Plant Production Systems, Wageningen University, Haarweg 333 6709 RZ, The Netherlands.
E-mail: N.Anten@bio.uu.nl

and Caldwell 1990, Anten and Ackerly 2001a), and increased nutrient or water availability to remaining tissues due to increased root:shoot ratios (Wareing et al. 1968). These processes would contribute to an increase in NAR, by enhancing photosynthetic rates. There are also a number of active physiological and allocational processes exhibited in response to defoliation that may contribute to compensatory growth. NAR may be enhanced by increases in leaf nitrogen concentration and other adjustments that increase light-saturated photosynthetic rates (Nowak and Caldwell 1984, Anten and Ackerly 2001a). LAR may be increased by activation of dormant buds and increased allocation to new leaf production (Oosterheld and McNaughton 1991, Trumble et al. 1993). Utilization of stored carbohydrates may play important roles in all of these compensatory processes (McPherson and Williams 1998). These processes may contribute to a greater RGR, which enables defoliated plants to recover the losses that were caused by defoliation (Hilbert et al. 1981).

The magnitude of the responses listed above and their significance for compensatory growth has been the subject of much debate (e.g., Hilbert et al. 1981, McNaughton 1983, Paige and Whitman 1987, Trumble et al. 1993). In most previous studies compensation has been quantified by comparing the performance of a defoliated plant to that of an undamaged individual (Hilbert et al. 1981, Oosterheld and McNaughton 1988, 1991, Ovaska et al. 1993, Mabry and Wayne 1997). This comparison has also been used to quantify the tolerance of plants to leaf damage, i.e., the ability to sustain growth or fitness following defoliation (see Stowe et al. 2000). While the comparison of defoliated and undamaged individuals measures the net impact of defoliation, it does not directly assess the functional role of compensatory responses. The ecological and evolutionary significance of compensatory responses is appropriately estimated by comparing the performance of defoliated plants to the estimated response of a hypothetical plant that is defoliated but does not possess any mechanisms of compensatory growth (see Anten and Ackerly 2001a). In this paper we use growth analysis methods to develop a new quantitative approach with which such comparisons can be made.

We conducted a greenhouse experiment with the palm *Chamaedorea elegans*, in which plants were subjected to different levels of defoliation and grown at two different light availabilities. *C. elegans* occurs strictly in the understory of tropical rain forest where light is a critical limiting resource. Leaves of many palm species, including *C. elegans*, are collected by local people and used for a variety of purposes (Reining et al. 1992). An understanding of the relationship between different levels of defoliation and the growth, reproduction, and survival of these palms is crucial to determine the demographic consequences and the sustainability of leaf harvesting. The work reported here is done in conjunction with a large-scale field study

that seeks to determine sustainable levels of leaf harvesting at the population level (D. D. Ackerly et al., *unpublished manuscript*).

In this experiment, we examined the effects of repeated defoliation over a long time period (two years), rather than responses to a single defoliation event as in many previous studies (e.g., Dyer 1975, Paige and Whitman 1987, Chazdon 1991, Mabry and Wayne 1997). This mimics the effects of continued harvesting, or of ongoing herbivory in natural populations, providing greater insight into the sustainability of leaf removal. Repeated defoliation reduces the role of short-term utilization of stored carbohydrates and focuses more on ongoing growth responses. We also examined responses under different light levels, roughly corresponding to understory vs. gap conditions that *C. elegans* plants experience at our field site in Chiapas, Mexico (Anten and Ackerly 2001a). Previous studies (Oosterheld and McNaughton 1988, 1991, Coughenour et al. 1990, Ovaska et al. 1993) have examined the influence of nutrient and water availability on compensatory responses, but light has received much less attention. Since defoliation directly impacts light harvesting, below- and aboveground resources may have different effects on mechanisms and levels of compensation.

The focus of this paper is the introduction of a new method to quantify the functional role of compensation, as described in the previous paragraphs, and this approach will be applicable to many studies of herbivory and plant responses to damage. We address the following questions: (1) To what extent and by what mechanisms are *C. elegans* plants able to mitigate the negative effects of repeated defoliation on growth and reproduction. (2) How does the importance of potential compensatory mechanisms change with defoliation level and light availability?

MATERIALS AND METHODS

Plant material

For this study we used the nonclonal dioecious tropical palm *Chamaedorea elegans*. *C. elegans* occurs in the understory of tropical rain forests in southeastern Mexico, Guatemala, and Belize up to an altitude of ~1400 m. It rarely becomes taller than 1.4 m (Hodel 1992). Leaves of *C. elegans* are harvested by local residents for the floral industry, mainly in North America. The intensity of harvesting differs widely depending on local practices. Leaf harvesters usually return to the same plant once or twice a year and remove 30–100% of the newly produced leaves (Reining et al. 1992). This species has a monopodial growth form with compound pinnate leaves born along a single erect stem. We distinguish the following parts for study of allocation: (1) lamina, which constitutes the leaflets; (2) rachis: defined here as the entire leaf support axis (rachis, petiole, and the sheathing leaf base; [see Chazdon 1986]); (3) stem, (4) roots, and (5) reproductive organs.

Experimental procedures

The experiment was carried out in the greenhouse at the Stanford University Plant Growth Facility, Stanford, California, USA. The plants for the greenhouse experiment were obtained from a commercial grower: Lailani Foliage, in Tohoa, Hawaii. They had been grown from seeds, collected from natural populations in Mexico, at ~30% of full daylight in 6.6-L pots filled with standard potting soil. The plants were between 33 and 36 months old when we received them (1 September 1997). There were 4–10 individuals in each pot, and they were thinned to one per pot for the experiment. They were then assigned to one of two light treatments, 16% and 5% of full daylight (“high-light” and “low-light”, respectively) created with neutral-density shade cloth (Hummert International, Earth City, Missouri, USA) and shading by the greenhouse roof. These light levels are close to the levels that plants experience in the field. For a large population in southern Mexico, Anten and Ackerly (2001a) found that plants in the understory received on average ~4% of full daylight. Those in medium-sized treefall gaps received ~14%. Six 2 × 3 m shade houses were arranged in three blocks, with a high-light and low-light treatment in each block.

As noted, this study was done in conjunction with a field study to determine sustainable levels of leaf harvesting. We therefore chose a number of defoliation treatments that would bracket the intensity of leaf harvesting, and match the treatments in our field experiment. Plants were assigned to one of five defoliation treatments in which, 0 (control, no leaves removed), 20, 33, 50, or 66% of the leaves were removed. There were 12 replicate plants per treatment, and in the 0, 33, and 50% treatments there was an extra set of 12 plants that were used to determine the allometric relationships for the nondestructive estimates of initial plant size. This resulted in a total of 276 individuals in the experiment (5 treatments × 2 light × 3 blocks × 4 reps × 2 harvests, plus 36 plants for allometry). Plants had been randomly assigned to a defoliation and light treatment.

Defoliation treatments were imposed one month after transplanting (6 October 1997), and continued for over one year before harvests were initiated to conduct growth analysis. The long preharvest period (~13 months) was to allow for plants to adjust to the defoliation regime and the greenhouse conditions so that the growth analysis did not reflect transient changes. Treatments were imposed by removing the youngest fully expanded leaf and then moving down the stem and removing every fifth (20%), every third (33%), every other (50%), and two out of every three leaves (66%). Subsequently, every three months we removed leaves according to the defoliation treatment, that is one out of every five, three, or two, or two out of every three newly produced leaves in the 20, 33, 50 and 66%

treatments, respectively. The frequency of harvesting was higher than in the field because leaf production rates were higher in the greenhouse. Removed leaves were divided into rachis and lamina. Rachis and lamina dry mass were determined after oven drying at 70°C for at least 72 hours and lamina area was determined with a leaf area meter (LI-3100, LI-COR, Lincoln, Nebraska, USA). On these occasions we also removed other dead parts from the plants (abscised leaves and reproductive organs) and determined their dry mass. Plants were fertilized four times (October 1997, March 1998, September 1998, February 1999) with 1.5 g of Peters 20-20-20 General Purpose fertilizer (Scotts Fertilizer, Marysville, Ohio, USA) dissolved in 10 mL of tap water for a total of 1.2 g of N, P, and K per plant; they were watered five times per week.

On 8 and 9 November 1998, we made the following nondestructive measurements on every plant to obtain estimates of the stem, rachis, and lamina mass as well as lamina area: stem diameter just below the lowest leaf, stem length from soil level to the base of the youngest leaf, the basal diameter and length of the rachis of every leaf, and the number of leaflets and the length of the longest leaflet for every leaf. It was not possible to obtain nondestructive estimates of reproductive organs and these were therefore removed. One day after completion of the nondestructive measurements, 12 high- and 12 low-light plants from the 0, 33, and 50% treatments were harvested. These plants were used to determine the allometric relationships between the nondestructive measurements discussed above and the actual size of the various plant parts. Plants were cut at ground level and divided into stem, leaf rachises, and leaf lamina. Stems were also divided into the external exposed part and the internal part, enclosed by the rachises. This distinction was important to make nondestructive estimates of stem mass more accurate. We were unable to separate the roots, because it was not possible to distinguish between the roots of a given plant and those of plants that had previously shared the same pot. Lamina area and the dry mass of individual organs were determined in the same way as discussed above. The allometric relationship used to estimate lamina mass and area was of the form $y = ax + b$, where x is the product of the number of leaflets on a leaf and the length of the longest leaflet, and a and b are coefficients. Stem and rachis mass (y) were estimated with a relationship of the form $y = c \ln(x) + d$, with x the product of the stem or rachis length and the square of the basal diameter, and c and d coefficients. In all cases r^2 was >0.88. The relationships to estimate lamina mass and area assume that the treatments had very little effect on specific leaf area (SLA). This assumption was justified by our data (Table 2).

The remaining plants were harvested destructively on 27 July 1999, 260 days after we had made the initial nondestructive size estimates on them. This relatively long period between the two harvests was chosen be-

cause *C. elegans* grows very slowly (RGR of $\sim 0.0025 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) (Anten and Ackerly 2001b). Lamina area and the mass of all aboveground parts were determined in the same way as in the first harvest. During this harvest it was also possible to determine root mass and belowground stem mass, because the roots of the plants that had initially shared the pot with the experimental plants had now completely decayed. The root system and belowground stem were carefully washed, separated from each other and weighed after oven drying for at least 72 hours at 70°C .

Growth analysis

Growth parameters were estimated with the iterative approach developed by Anten and Ackerly (2001b), with modifications to enable us to estimate allocation to reproductive organs. Unlike other methods of growth analysis (i.e., the classical and functional approaches), this method can be used to conduct growth analysis on plants that have lost significant amounts of mass and leaf area between successive harvests (see Anten and Ackerly 2001b). Details of this approach are given in Anten and Ackerly (2001b); here we only give a brief description.

The approach determines average values for the following growth parameters by means of iteration: absolute growth rate (G , g/d), relative growth rate (RGR, $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$), net assimilation rate (NAR, $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), lamina mass ratio (lamina mass/total mass, LMR, g/g), lamina area ratio (LAR, m^2/g), the daily change in the average SLA of plants (ρ , day^{-1}) and the fraction of newly assimilated biomass that is allocated to the production of lamina tissue (f_{lam} , g/g) or reproductive organs (f_{rep} , g/g). Given initial biomass and leaf area, and the dates and amounts of leaf area lost during the growth interval, it uses a number of growth functions and searches the parameter space to find the joint solution of parameter values that yield values for the total plant mass, leaf lamina mass, and lamina area at the end of the growth period that match the measured values. The method solves directly for NAR, f_{lam} , f_{rep} , and γ , the proportional difference between the mean SLA of newly produced leaves and standing leaves.

Definition and analysis of compensation

The main problem with quantifying compensatory growth involves the choice of a suitable null model for the potential negative effect of defoliation with which the observed performance of defoliated plants can be compared. The null model that is most commonly used is that the relative growth rate (RGR) should be unaffected by defoliation, though the absolute growth rate will decline due to the reduction in leaf area. Compensatory growth is therefore defined as an increase in RGR of defoliated plants relative to undamaged individuals (see *Introduction*). With a greater RGR, defoliated plants will eventually recover their loss (Hilbert et al. 1981). In our view this is not an appropriate

definition. Defoliation of a given plant results in a reduction of its LAR and thus RGR as well. The plant may respond through compensatory mechanisms (e.g., increased photosynthesis of remaining leaves or increased allocation to new leaves), which may result in an increase in net assimilation rate (NAR) and/or a partial recovery of the LAR. Yet this response may not be enough to compensate for the negative effect of the initial reduction in LAR on RGR. This plant will therefore have a lower RGR than an undamaged plant, but it will have a higher RGR than it would have if it had not responded to defoliation in any way.

Here, we define the potential negative effect of defoliation (L_{pot}) as the difference between the performance of an undamaged plant ($\Pi_{\text{u}}(x_{\text{u}})$) and the predicted performance of a hypothetical noncompensating defoliated plant ($\Pi_{\text{o}}(x_{\text{u}})$):

$$L_{\text{pot}} = \Pi_{\text{u}}(x_{\text{u}}) - \Pi_{\text{o}}(x_{\text{u}}). \quad (1)$$

The real negative effect of defoliation (L_{real}) is the difference between the performance of an undamaged plant and the observed performance of a defoliated one ($\Pi_{\text{d}}(x_{\text{d}})$):

$$L_{\text{real}} = \Pi_{\text{u}}(x_{\text{u}}) - \Pi_{\text{d}}(x_{\text{d}}) \quad (2)$$

where Π is the performance measure (growth, plant size, reproduction etc.), x refers to a series of growth parameters that may change as a result of compensatory mechanisms (e.g., net assimilation rate NAR or allocation of mass to leaves), the subscripts d and u indicate whether a plant has been defoliated (d) or not (u). $\Pi_{\text{o}}(x_{\text{u}})$ refers to the performance of a defoliated plant with the growth parameter values of an undamaged plant (thus the x_{u} in parentheses). Compensation (C) is now defined as the fraction of the potential loss (L_{pot}) that is made up for by compensatory growth:

$$\begin{aligned} C &= [(L_{\text{pot}} - L_{\text{real}})/L_{\text{pot}}] \times 100\% \\ &= \{[\Pi_{\text{d}}(x_{\text{d}}) - \Pi_{\text{o}}(x_{\text{u}})]/[\Pi_{\text{u}}(x_{\text{u}}) - \Pi_{\text{o}}(x_{\text{u}})]\} \times 100\% \end{aligned} \quad (3)$$

where $C > 100\%$ indicates overcompensation, $C = 100\%$ full compensation, $0 < C < 100\%$ partial compensation, $C = 0\%$ no compensation, and $C < 0\%$ negative compensation. Note the similarity between the definitions of compensation introduced here for whole-plant performance and the definition we have suggested for photosynthetic compensation (Anten and Ackerly 2001a).

In this study we consider four measures of performance (Π): the final aboveground mass and the total growth of aboveground parts, leaf laminae, and reproductive structures between the first and second harvests. For the control and the defoliated plants these measures can be easily determined to obtain $\Pi_{\text{u}}(x_{\text{u}})$ and $\Pi_{\text{d}}(x_{\text{d}})$, respectively (see Eqs. 1–3). Aboveground mass is directly measured and the growth values are deter-

mined with the iterative approach outlined above. To estimate the performance of a hypothetical noncompensating defoliated plant ($\Pi_0(x_u)$), we assume the biomass, lamina area, and the associated ratios (e.g., LAR) at the initial harvest as well as the loss of leaf mass and lamina area between the two harvests (due to harvesting and natural leaf abscission) to be equal to that of defoliated plants. The growth parameters: NAR, the allocation of mass to leaf laminae (f_{lam}) and reproductive organs (f_{rep}) and fractional difference between the SLA of new and standing leaves (γ) on the other hand, are taken to be equal to those of control plants. In addition we assume the loss of reproductive mass (i.e., dead reproductive organs that are dropped from the plant) to be equal to that of control plants too, because it is a direct consequence of changes in f_{rep} . Note that taking loss of reproductive mass equal to either defoliated or control plants did not significantly affect the results in this study. The mass and growth values that serve as measures for $\Pi_0(x_u)$ are then calculated with the iterative approach. The values of $\Pi_u(x_u)$, $\Pi_d(x_d)$ and $\Pi_0(x_u)$ thus obtained are substituted into Eqs. 1–3 to obtain estimates of compensatory growth.

It is also of interest to estimate the relative contribution of changes in each individual parameter to the overall extent of compensation (see Anten and Ackerly 2001a). To achieve this, we conducted a sensitivity analysis of the performance of defoliated plants by assuming one of the four growth parameters (see *Growth analysis*) to be equal to the measured value for defoliated plants, while the other three were taken to be equal to those of control plants. Compensation was then calculated by replacing $\Pi_d(x_d)$ in Eq. 3 by the estimated performance value.

In addition to C , we also calculate the ratio $\Pi_d(x_d)/\Pi_0(x_u)$ between the performance of a defoliated plant ($\Pi_d(x_d)$) and the performance of a hypothetical noncompensating plant ($\Pi_0(x_u)$), as a measure of the relative increase in growth resulting from compensatory responses.

Statistical analysis

This experiment utilized a split-plot design, with one factor assigned to subplots (light levels within blocks) and a second factor (defoliation treatment) fully randomized among individuals within subplots. For analysis of variance, block is considered a random factor, and the light effect ($df = 1$) is tested over the light by block interaction ($df = 2$). It is necessary to assume that there is no interaction between defoliation and block (Steel and Torrie 1980), and the defoliation effect and light by defoliation interaction (both $df = 4$) are both tested over the error term. We were able to obtain growth analysis parameters for each plant individually, because the initial measurements were done nondestructively, so these were also analyzed by ANOVA.

This design provides much greater statistical power to detect effects of the fully randomized factor (defo-

TABLE 1. Measured values of plant parameters, including lamina area ratio (LAR), lamina mass ratio (LMR), and root mass at the final harvest.

Plant and defoliation parameters	Parameter values	
	High light	Low light
Total mass (g)		
Control	167.2 (14.5)	138.0 (15.0)
20%	157.9 (11.9)	117.1 (11.2)
33%	110.1 (7.3)	103.0 (7.3)
50%	101.1 (6.2)	83.7 (6.3)
66%	82.4 (6.1)	55.2 (5.7)
Lamina mass (g)		
Control	29.1 (2.2)	30.7 (3.9)
20%	27.8 (1.9)	24.5 (2.2)
30%	20.2 (2.3)	22.4 (1.9)
50%	20.1 (1.6)	19.5 (1.1)
66%	15.1 (1.5)	11.0 (0.9)
Lamina area (m ²)		
Control	0.529 (0.041)	0.549 (0.059)
20%	0.464 (0.028)	0.438 (0.033)
33%	0.352 (0.039)	0.398 (0.030)
50%	0.336 (0.030)	0.355 (0.022)
66%	0.238 (0.022)	0.209 (0.017)
LAR (m ² /kg)		
Control	3.23 (0.16)	4.01 (0.23)
20%	3.00 (0.14)	3.82 (0.21)
33%	3.17 (0.22)	4.11 (0.36)
50%	3.34 (0.22)	4.33 (0.25)
66%	2.93 (0.18)	4.19 (0.13)
LMR (g/g)		
Control	0.177 (0.007)	0.220 (0.010)
20%	0.178 (0.009)	0.215 (0.011)
33%	0.183 (0.016)	0.224 (0.010)
50%	0.199 (0.011)	0.237 (0.009)
66%	0.181 (0.011)	0.206 (0.009)
Root mass (g)		
Control	55.1 (6.0)	30.9 (3.7)
20%	48.6 (4.9)	24.6 (2.7)
33%	32.8 (3.4)	23.5 (3.0)
50%	30.3 (2.0)	20.5 (1.9)
66%	24.0 (2.9)	13.5 (1.6)

Note: Values in parentheses are ± 1 SE ($n = 12$).

liation) compared to the split-plot factor (light), which corresponded to our greater interest in the former. As a result some quantitatively large effects of light are only marginally, or are not, statistically significant.

RESULTS

Standing mass and lamina area

Defoliation had a significant negative effect on total and aboveground mass, mass of individual organs (lamina, rachis, reproductive, stems and roots) and lamina area at the final harvest (Tables 1 and 2; data for reproductive, stem, and rachis mass not shown). This negative effect was also apparent at the initial harvest (Table 2), although root mass and total plant mass could not be determined at this stage. Recall that at the initial harvest the plants had already been subjected to about one year of sustained defoliation, and the mass and area data are based on nondestructive estimates (see

TABLE 2. Results of analysis of variance with defoliation (df = 4) and light (df = 1) as factors (i.e., for the defoliation \times light interaction, df = 4).

Dependent variable	Defoliation <i>P</i>	Light <i>P</i>	Light \times defoliation <i>P</i>
Standing mass and estimated ratios			
Initial harvest			
Aboveground mass	<0.0001***	0.886	0.550
Aboveground LAR	<0.0001***	0.760	0.829
Aboveground LMR	<0.0001***	0.982	0.842
SLA	0.711	0.556	0.536
Final harvest			
Total mass	<0.0001***	0.0133*	0.577
Aboveground mass	<0.0001***	0.174	0.664
Lamina mass	<0.0001***	0.273	0.531
Lamina area	<0.0001***	0.522	0.810
LAR	0.131	0.0323*	0.935
LMR	0.0066**	0.031*	0.944
SLA	0.251	0.0510	0.251
Root mass	<0.0001***	0.0321*	0.063
Lamina area/root mass†	0.523	0.001**	0.967
Estimated growth parameters			
RGR	0.0491*	0.0101*	0.0342*
NAR†	0.0292*	0.0062**	0.0347*
ρ	0.356	0.0053**	0.0168*
LAR _{av}	0.0131*	0.177	0.796
f_{lam} †	<0.0001***	0.368	0.774
Rachis allocation	0.0959	0.519	0.780
Stem allocation	0.0464	0.0112	0.414
Reproductive allocation†	0.0305*	0.655	0.948
Estimated absolute growth			
Total growth	<0.0001***	0.0153*	0.919
Lamina growth	0.855	0.0592	0.471
Leaf production	0.0136**	0.103	0.841
Total loss of biomass	<0.0001***	0.0333*	0.531
Loss of lamina biomass (defoliation and abscission)	0.0114*	0.0226*	0.573

Notes: RGR is relative growth rate, NAR is net assimilation rate, LAR is lamina area ratio, LAR_{av} is the average LAR during the growth period, f_{lam} is the fraction of biomass allocated to lamina growth, SLA is the lamina area per unit lamina mass, and ρ is the daily change in the average specific leaf area SLA of the plant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† These values were square-root transformed.

Materials and methods). Total mass was less at high light than at low light (Tables 1 and 2).

Defoliation had a significant negative effect on aboveground LAR (lamina area/aboveground mass) at the initial harvest (Table 2). But at the final harvest, neither the aboveground LAR (data not shown) nor the total LAR (lamina area/total mass) was significantly related to defoliation (Tables 1 and 2). At the final harvest, low-light plants had a significantly higher LAR than high-light plants (Tables 1 and 2), which was mostly the result of differences in lamina mass per unit total mass (LMR). SLA did not differ between treatments.

Root mass decreased significantly with increasing level of defoliation. However, the magnitude of this reduction was similar to the magnitude of the reduction in lamina area, and as a result the total leaf area per unit root mass (area/root, hereafter) did not differ between defoliation treatments. Low-light plants had a significantly higher leaf area/root mass ratio than high-light plants (Table 2).

Growth, biomass allocation, and biomass losses

Aboveground growth rates decreased significantly with defoliation and were also lower for the low- than for the high-light plants (Tables 2 and 3). Hereafter growth refers to aboveground growth only, because we did not determine root mass at the initial harvest. In contrast to total growth, lamina growth did not differ between defoliation treatments (Tables 2 and 3). The reduction in growth of defoliated plants relative to control plants was the result of significant reductions in the growth of stems, rachises, and reproductive organs (Tables 2 and 3). Control plants produced slightly but significantly more leaves than the defoliated plants but light availability did not affect leaf production rates (Tables 2 and 3).

The total amount of biomass that was lost by natural abscission during the growth period (due to loss of dead leaves and reproductive organs) decreased significantly with the level of defoliation and was greater at high than at low light (Table 2). Total leaf loss, i.e., defoliated

TABLE 3. Average estimated daily growth rates (with 1 SE in parentheses; $n = 12$) of all aboveground parts and of leaves (lamina + rachis), laminas, stems, and reproductive organs as well as leaf production rates.

Plant and defoliation parameters	Growth rate	
	High light	Low light
Aboveground growth (g/d)		
Control	0.232 (0.037)	0.177 (0.029)
20%	0.230 (0.023)	0.171 (0.027)
33%	0.179 (0.012)	0.139 (0.021)
50%	0.158 (0.006)	0.104 (0.012)
66%	0.146 (0.006)	0.055 (0.007)
Leaf growth (g/d)		
Control	0.124 (0.0283)	0.103 (0.0225)
20%	0.117 (0.0094)	0.100 (0.0170)
33%	0.104 (0.0104)	0.079 (0.0132)
50%	0.091 (0.0048)	0.065 (0.0085)
66%	0.086 (0.0037)	0.040 (0.0064)
Lamina growth (g/d)		
Control	0.0380 (0.0110)	0.0337 (0.0071)
20%	0.0445 (0.0026)	0.0364 (0.0061)
33%	0.0399 (0.0051)	0.0319 (0.0059)
50%	0.0451 (0.0038)	0.0341 (0.0040)
66%	0.0487 (0.0032)	0.0205 (0.0029)
Leaf production (leaves/yr)		
Control	6.03 (0.59)	4.97 (0.35)
20%	5.63 (0.44)	5.14 (0.14)
33%	4.66 (0.33)	4.30 (0.33)
50%	5.04 (0.24)	4.45 (0.25)
66%	5.42 (0.36)	3.97 (0.40)
Stem growth (g/d)		
Control	0.0865 (0.0181)	0.0697 (0.0159)
20%	0.0725 (0.0074)	0.0632 (0.0114)
33%	0.0639 (0.0070)	0.0470 (0.0087)
50%	0.0455 (0.0034)	0.0308 (0.0051)
66%	0.0376 (0.0039)	0.0197 (0.0039)
Reproductive growth (g/d)		
Control	0.0546 (0.0077)	0.0393 (0.0029)
20%	0.0522 (0.0086)	0.0370 (0.0071)
33%	0.0404 (0.0048)	0.0321 (0.0060)
50%	0.0314 (0.0048)	0.0248 (0.0039)
66%	0.0263 (0.0043)	0.0086 (0.0021)

leaves plus leaves lost through abscission, was significantly greater at high than at low light and decreased with increasing intensity of defoliation (Table 2).

Average RGR and NAR values increased with the level of defoliation at high light but not at low light (Fig. 1a, b). Defoliation had a significant effect on NAR and a marginally significant effect on RGR, while the light \times defoliation interaction was significant for both parameters. High-light plants had significantly higher RGR and NAR values than low-light plants (Table 2). The fractional allocation of new mass to the production of lamina tissue (f_{lam}) increased considerably with the level of defoliation (Fig. 1d, Table 2). Light availability, on the other hand, had no effect on f_{lam} . The fractional allocation of mass to the production of rachises, stems, and reproductive organs all decreased with defoliation (Table 2, Fig. 1f). The average estimated LAR during the growth period (LAR_{av}) was not strongly af-

ected by defoliation. The significant defoliation effect was mostly due to the fact that the high-light 66% defoliated plants had lower LAR_{av} values than the other plants (Fig. 1c, Table 2).

For all treatments, average SLA decreased over time (Fig. 1e). The extent to which defoliation affected this decline differed between light treatments. In the high-light treatment, ρ became more negative with the level of defoliation, while in the low-light treatment it became slightly less negative (significant defoliation by light interaction $P < 0.05$, Table 2).

Compensation

Fig. 2 shows the performance (final aboveground mass, aboveground growth, lamina growth, and growth of reproductive organs) of defoliated ($\Pi_d(x_d)$) and control plants ($\Pi_u(x_u)$), and the performance of hypothetical noncompensating defoliated plants ($\Pi_0(x_u)$, see *Definition and analysis of compensation*) as a function of the level of defoliation. In general, defoliated plants did not perform as well (i.e., had lower mass or growth rates) as control plants but performed considerably better than hypothetical noncompensating plants. It was thus calculated with Eq. 3 that changes in NAR, f_{lam} , ρ , and f_{rep} in defoliated plants resulted in partial compensation ($0 < C < 1$) of the potential loss in performance caused by defoliation (Fig. 3). The degree of compensation tended to decrease with the level of defoliation and was generally greater at high than at low light availability. Compensation also depended on the measure of performance. It was greatest for lamina growth, with C ranging from 60% partial compensation to 200% overcompensation, followed by total aboveground growth ($C = 14$ –89%) and total aboveground mass ($C = 7$ –90%), while it was lowest for reproductive growth ($C = -3$ to 23%).

Fig. 4 shows the relative contributions of changes in two of the individual growth parameters, NAR and f_{lam} , to the compensation of losses in either total growth rates or lamina growth rates. Contributions of changes in the other two parameters (ρ and f_{rep}) were negligible or negative. At high light, increased NAR contributed more to compensation in total growth than changes in f_{lam} , but this difference was greater at 20% defoliation than at higher levels (Fig. 4a). At low light, NAR had a greater effect than f_{lam} at low levels of defoliation but not at high levels. The comparatively greater importance of NAR for compensation was in spite of the fact that increases in NAR with defoliation were smaller than increases in f_{lam} (Fig. 1). This is because an increase in NAR results in a proportional increase in RGR: ($RGR = NAR \times LAR$). In contrast, an increase in f_{lam} has a less than proportional effect on RGR because f_{lam} is the amount of new biomass that is allocated to leaf production, and effects on LAR only accumulate over time. Compensation in lamina growth was more strongly related to increases in f_{lam} than to increases in NAR (Fig. 4c, d). This is because changes in f_{lam} have

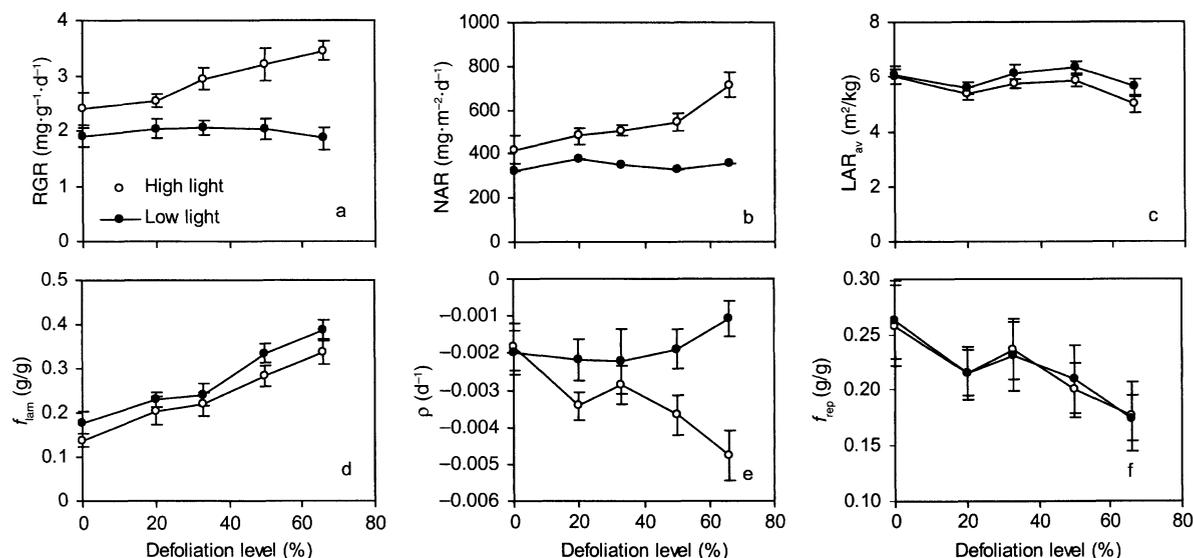


FIG. 1. (a) The estimated average relative growth rate (RGR), (b) the net assimilation rate (NAR), (c) the average leaf area ratio during the growth period (the period from the initial to the final harvest; LAR_{av}), (d) the fractional allocation of mass to lamina growth (f_{lam}), (e) the daily change in the average SLA of the plant (ρ), and (f) fractional allocation of mass to reproductive organs (f_{rep}) for *Chamaedorea elegans* plants subjected to different levels of defoliation and grown at either of two light levels. Bars indicate ± 1 SE ($n = 12$).

relatively larger effect on lamina growth than on total growth.

The ratio between the observed performance and the estimated performance of hypothetical noncompensating plants ($\Pi_d(x_d)/\Pi_0(x_u)$) increased with both the level of defoliation and with light availability (Fig. 5). This ratio depended on the measure of performance in the same way as compensation; $\Pi_d(x_d)/\Pi_{d,0}(x_u)$ had the highest values for lamina growth followed by total aboveground growth, aboveground mass, and reproductive growth.

DISCUSSION

Compensatory mechanisms and their importance for plant performance

We developed a framework with which compensatory growth of defoliated plants was quantified relative to the growth of hypothetical noncompensating defoliated plants. This approach differs from the commonly used one where compensatory growth of defoliated plants is quantified relative to undamaged individuals (Hilbert et al. 1981, Oosterheld and McNaughton 1989, 1991, Ovaska et al. 1993). The difference between the two approaches becomes apparent when considering the results for the low-light treatment, where RGR values of defoliated plants were not significantly different from those of the control plants. The commonly used approach would consequently lead one to conclude that at low light defoliated plants did not compensate for the losses caused by defoliation. However, defoliation causes an initial reduction in LAR, so even the maintenance of RGR requires compensatory responses. The

defoliated plants allocated a considerably larger fraction of their mass to lamina production (f_{lam}), and there was a smaller increase in net assimilation rate (NAR). With our approach we could show that as a result of this, they performed considerably better in terms of growth, final mass, and reproduction than hypothetical noncompensating plants, and that they were able to compensate for a significant fraction of the potential loss in performance caused by defoliation (see Figs. 2 and 3).

The increase in the fractional allocation of mass to lamina growth (f_{lam}) with defoliation is consistent with various other studies (e.g., Hilbert et al. 1981, Oosterheld and McNaughton 1989, 1991, Rosenthal and Kotanen 1994). An increase in f_{lam} after partial defoliation is an important compensatory mechanism because it results in an increase in the ratios of lamina mass and area to total mass (LMR and LAR, respectively), both of which are reduced due to defoliation. In this study LMR and LAR values of defoliated plants were indeed restored to values similar to those of undamaged plants in spite of the fact that plants were repeatedly defoliated. As a result of their greater f_{lam} , defoliated plants maintained relatively high rates of leaf production (in terms of leaf numbers), even when their growth was strongly reduced. This has important implications for leaf harvesters.

The increase in f_{lam} after defoliation probably resulted from both an increase in allocation of new assimilates to lamina growth at the expense of other organs and the utilization of stored carbohydrates. Understory plants tend to store relatively large amounts of car-

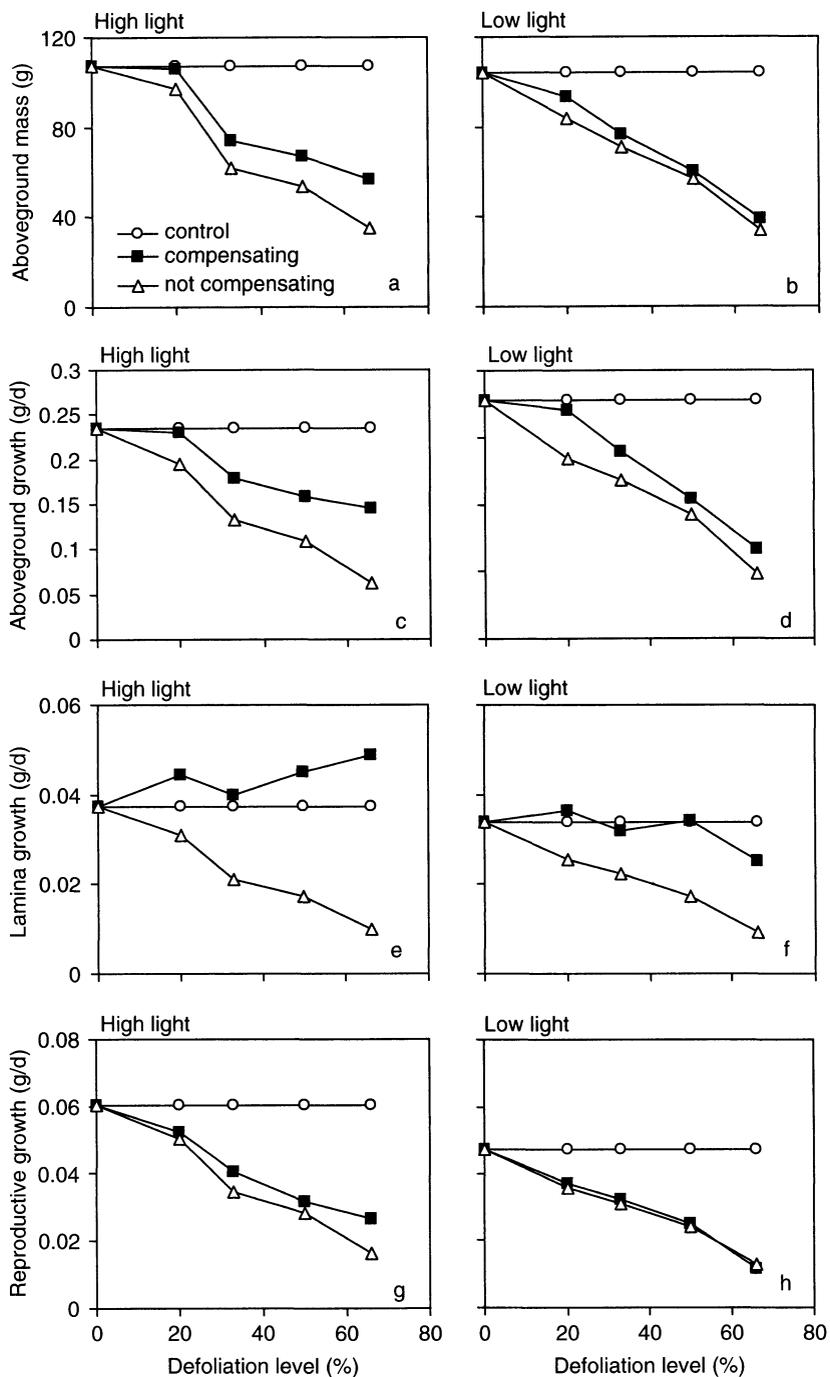


FIG. 2. Average aboveground mass at the final harvest (a,b), aboveground growth (c,d), lamina growth (e,f), and growth rates of reproductive organs (g,h) of control and defoliated plants as a function of the level of defoliation. These same values were estimated for defoliated plants assuming them to have the growth parameter values (NAR , f_{lam} , ρ , and f_{rep}) of control plants (hypothetical noncompensating plants, $\Pi_0(x_u)$); for calculation procedure see *Materials and Methods: Definition and analysis of compensation*). In the key, “compensating” refers to observed performance of defoliated plants (i.e., defoliated plants with compensatory mechanisms), and “not compensating” refers to $\Pi_0(x_u)$ (hypothetical noncompensating plants). For control and defoliated plants only averages are shown, and the $\Pi_0(x_u)$ values are calculated using average mass, leaf area, and growth parameter values.

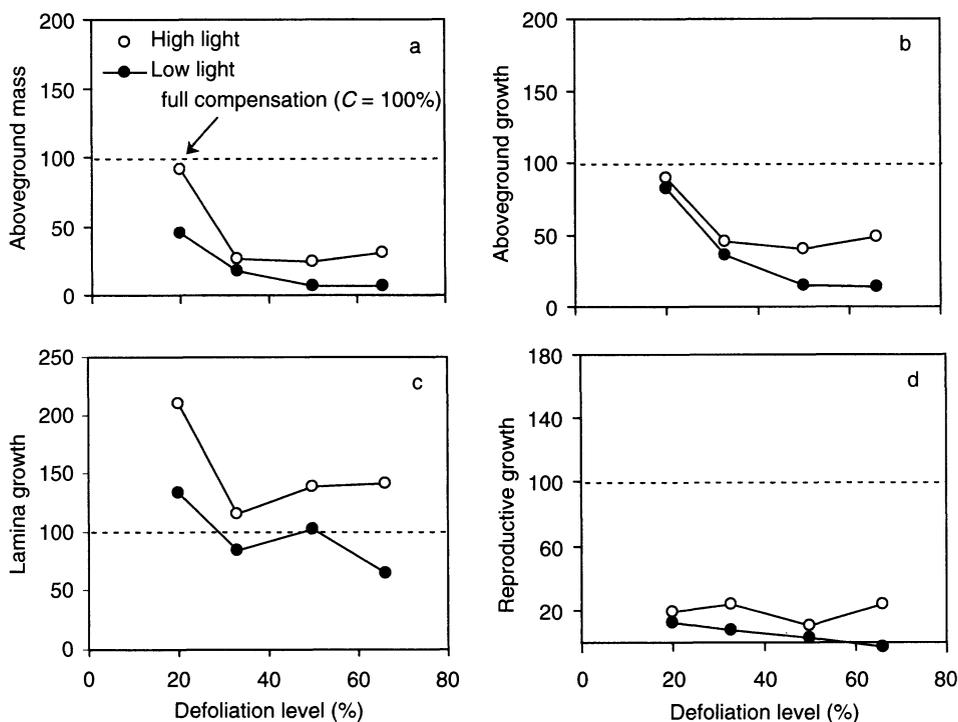


FIG. 3. The percentage of the potential loss in (a) final aboveground mass, (b) aboveground growth, (c) lamina growth, and (d) reproductive growth compensated for by compensatory responses to defoliation (i.e., C as calculated with Eq. 3). The dashed lines indicate full compensation ($C = 100\%$).

bohydrates in their stems, roots, or other organs (Kobe 1997, Canham et al. 1999). These carbohydrates contribute to regrowth of leaves after defoliation and to the maintenance of remaining structures. It has been shown that plants with high predefoliation levels of stored carbohydrates grew more rapidly and had higher probabilities of survival after defoliation than those with lower levels (McPherson and Williams 1998).

It is generally believed that there is a functional equilibrium between the size and activity of the root system (which supplies water and nutrients for photosynthesis) and the size and activity of the canopy (which supplies the assimilates that are used for root growth and nutrient uptake) (Brouwer 1962). We found that the ratio of leaf area to root mass (area/root ratio) did not differ between plants of different defoliation treatments, which was also shown by Brouwer (1962). Apparently, when the functional equilibrium between roots and leaves is disrupted due to a reduction in total leaf area through defoliation, allocation to roots and leaves is readjusted to restore the equilibrium. Our results demonstrate that this can occur even when reductions in total leaf area are frequent and severe.

Defoliation resulted in an increase in aboveground growth per unit leaf area (NAR) at high light but not at low light. Other studies (Oosterheld and McNaughton 1988, 1991) have also reported increases in NAR in defoliated grasses. For the plants used in this study,

Anten and Ackerly (2001a) showed that defoliation resulted in an increase in daily carbon gain per unit leaf area, which was probably an important determinant of the increased NAR found here. At high light, this increase in carbon gain was the result of both an increase in light-saturated photosynthetic rates (P_{max}) and of improved light penetration into the canopy. By contrast, in the low-light treatment, due to light limitation on photosynthesis, an increase in (P_{max}) had no effect on daily carbon gain and there was only an effect on self-shading (Anten and Ackerly 2001a). As a result, the increase in average per unit area carbon gain was greater at high than at low light, and this could explain the interactive effect of light and defoliation on NAR reported here.

NAR depends not only on the carbon balance of leaves but also on the amount and respiratory rate of nonphotosynthetically active tissue (Poorter 1990). Defoliation reduces the amount of leaf area relative to the amount of nonphotosynthetically active tissue and will therefore tend to increase the rate of whole-plant respiration per unit leaf area, which, in turn, negatively affects NAR.

In this study we were unable to estimate root growth, and the estimates of RGR, NAR, and f_{lam} reported here are based on aboveground growth. At the final harvest, defoliated plants had a lower root mass than control plants, which indicates that defoliation had resulted in

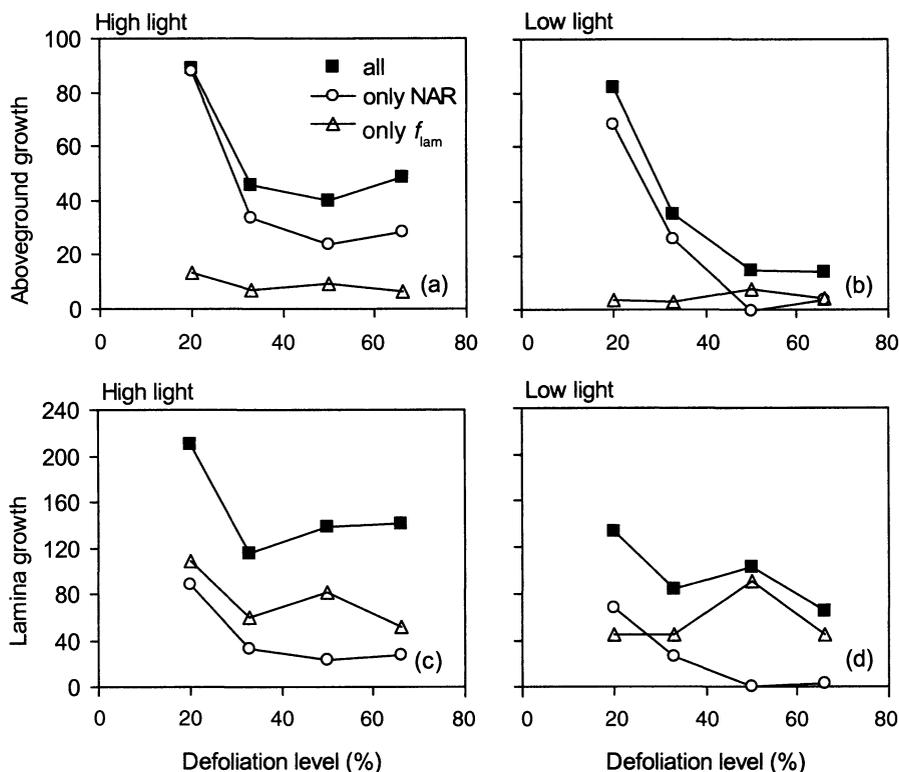


FIG. 4. Percentage compensation of losses in aboveground growth (a,b) or lamina growth (c,d) brought about by increases only in net assimilation rates (NAR) or only in fractional allocation of new mass to lamina production (f_{lam}), calculated for the high-light (a,c) and the low-light treatment (b,d). Calculated compensation resulting from changes in all four growth parameters (NAR, f_{lam} , ρ , f_{rep} ; see *Materials and Methods: Definition and analysis of compensation*) are included for reference ("all," taken from Fig. 3).

reduced root growth and loss of stored carbohydrates from the roots. This is consistent with Brouwer (1962), although other studies (Oosterheld and McNaughton 1988, 1991, Ovaska et al. 1993) found that defoliation had very little effect on root growth. The reduced root growth in defoliated plants found in this study implies that the positive effects of defoliation on NAR at the whole-plant level would be less than the enhancement we observed in aboveground NAR. By contrast, the positive effect of defoliation on f_{lam} based on total growth would be greater than its positive effect based on aboveground growth.

The observed increases in NAR with defoliation contributed more to compensation for losses in growth and final mass than the increases in allocation of mass to lamina production (f_{lam}), even though the increases in NAR with defoliation were smaller than those in f_{lam} (Fig. 4). However, the relative contribution of an increased f_{lam} became greater at higher levels of defoliation, mainly because f_{lam} itself increased with defoliation, and was greater at low than at high light. These results suggest that physiological changes that are related to enhancement of NAR, such as increases in leaf photosynthesis, tend to be the most important factor for compensation in growth and final mass. Apparently

even small increases in leaf photosynthesis can make a relatively large contribution to compensatory growth. But the contribution of shifts in allocation that result in greater f_{lam} increases with the level of defoliation and at lower light levels. Above we noted that under very shaded conditions photosynthesis is strongly light limited, and an increase in photosynthetic capacities of remaining leaves, a typical compensatory response to defoliation, will have little impact on whole-plant daily carbon gain. Under these conditions the potential for increasing NAR is probably lower and plants will have to rely more on changes in allocation and the availability of stored carbohydrates to mitigate the damage caused by leaf loss.

The estimated degree of compensation (C) differed depending on the measure of performance: final plant mass, and total, lamina, and reproductive growth (Figs. 2 and 3). For example, defoliated plants were able to fully compensate for the loss in lamina growth, while they compensated for <20% of the loss in reproductive output. This was because of the increase in allocation to lamina growth in the defoliated plants at the expense of allocation to other functions, particularly reproduction. Note that we did not distinguish between male and female plants, which may have different repro-

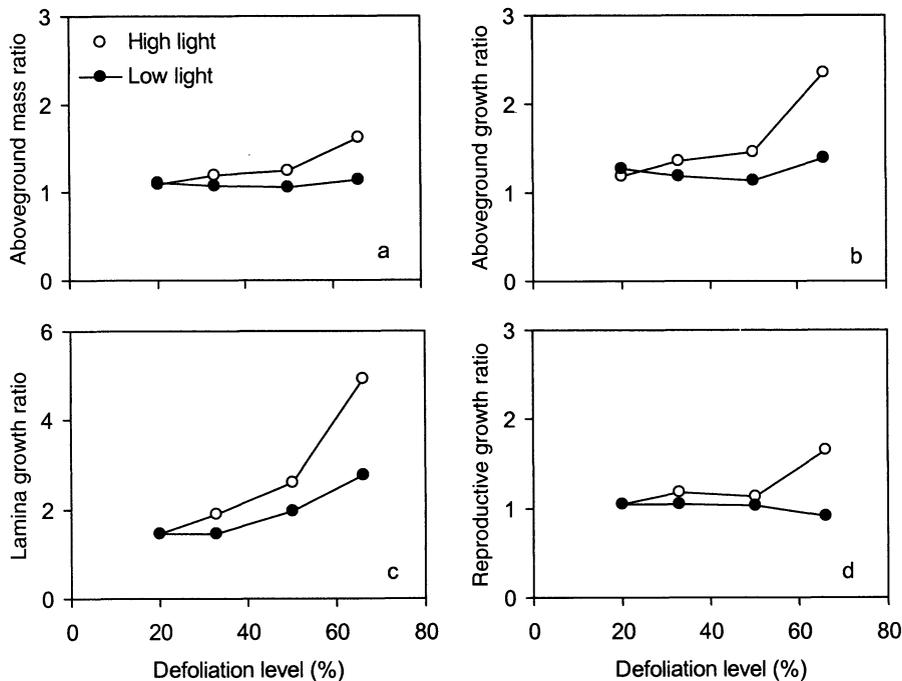


FIG. 5. The ratio $[\Pi_d(x_d)/\Pi_0(x_u)]$ between the performance of defoliated plants and the estimated performance of hypothetical noncompensating defoliated plants. As performance measures we show (a) final aboveground mass, (b) aboveground growth, (c) lamina growth, and (d) reproductive growth. Note that the y-axis scaling in (c) is different from the other panels.

ductive outputs. These differences were probably smaller in the greenhouse than they would be in the field, because the greenhouse females did not mature any fruit.

Lamina growth, reproduction, and final mass are performance measures of individual plants. The ecological implications of defoliation and compensatory growth, however, should ultimately be analyzed at the level of the population. As noted, this study was done in conjunction with a demographic study on natural populations of *C. elegans* in southern Mexico, in which fecundity, survival and transition probabilities, and population growth were estimated under different defoliation levels (N. P. R. Anten, unpublished data). In the field study, defoliation resulted in a strong reduction in reproduction but had only a small effect on leaf production, similar to the greenhouse results. Care should be taken, however, when comparing between greenhouse and field-grown plants, because growth conditions and related growth rates can differ considerably. Interestingly, survival of field plants was much more strongly correlated with the amount of leaf area of a plant than with any other factor (such as plant height, light availability, soil depth, or gender). With a matrix population model, population growth was very sensitive to changes in survival and relatively insensitive to changes in fecundity (N. P. R. Anten, unpublished results), a result that is consistent with other population studies on long-lived slow-growing organ-

isms (e.g., De Kroon et al. 2000, Zuidema 2000). Under the extremely light-limited conditions in the rain forest, understory plants can only grow very slowly and their potential reproductive output is similarly low. On the other hand, the comparatively stable climate in the rain forest allows for a relatively high annual rate of survival. Under these conditions, when plants are damaged it might be more important for them to respond through mechanisms that enable them to survive than through mechanisms that would safeguard reproduction.

Effects of light availability on compensatory growth

The ratio between the observed performance and the performance of hypothetical noncompensating plants ($\Pi_d(x_d)/\Pi_0(x_u)$; Fig. 5), as well as the degree of compensation (C), were estimated to be greater at high than at low light. Thus, the difference in performance between a defoliated plant possessing compensatory mechanisms and a similarly defoliated one that does not possess such mechanisms increases with light availability. This suggests that selection for compensatory responses should be favored more at high light. As a result of the lower ability of *C. elegans* to compensate at low light, the decline in performance with increasing levels of defoliation was stronger at low than at high light. The reaction norm of plant performance across a range of levels of defoliation indicates the degree of tolerance of plants to leaf damage (Stowe et al. 2000). Our results thus show that *C. elegans* is more tolerant

to leaf damage at high than at low light. Since gaps are infrequent, most of the plants in a natural population experience relatively low light levels, so overall tolerance levels in the population may be low.

In contrast with these results, other studies (Hilbert et al. 1981, Coley et al. 1985, Oosterheld and McNaughton 1989, 1991, Coughenour et al. 1990) have found that the negative effects of defoliation on growth increase with resource availability. This discrepancy might be explained by the fact that those studies only looked at the relationship between compensatory growth and availability of belowground resources, water and mineral nutrients, while the present study focused on light availability. Defoliation results in a reduction in the shoot-to-root ratio and consequently tends to enhance the nutrient supply and water status of remaining leaves (McNaughton 1983, Coughenour et al. 1990). As a result defoliation can ameliorate the effects of water or nutrient limitation (Coughenour et al. 1990). By contrast, defoliation aggravates the negative effects of light limitation because it directly reduces the ability of plants to capture light.

ACKNOWLEDGMENTS

We thank Hans Cornelissen and Lourens Poorter for comments on the manuscript, Barbara Lilley for technical and logistical support, and Taryn Fransen, Laura López-Hoffman, Becky Shaftel, and Kathleen Starmer for their assistance during the harvest and census work. This work was supported by the National Science Foundation (grant IBN 9604030).

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